TAXONOMY, VARIATION, AND CHOROLOGY OF THREE CHROMOSOME RACES OF THE CALAMAGROSTIS CANADENSIS COMPLEX IN ALASKA

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Calamagrostis canadensis (Michx.) Nutt. (Bluejoint) is one of the most important native grasses in the herbland economy of subarctic Alaska. It predominates in tall grasslands of southcentral and southwestern Alaska and is prominent in other mixed forb and grass communities. *Calamagrostis canadensis* demonstrates a wide ecological amplitude, occurring in lowland wet areas to windswept alpine ridges and in all major geographic regions from southeastern to arctic Alaska. It is rare or infrequent, however, in the Arctic (Wiggins and Thomas, 1962; Johnson, et al., 1966) and absent from the high Arctic (Porsild, 1957). The grass, considered in the wide sense, is circumpolar in distribution (Hultén, 1962).

Taxonomic treatments of this complex generally recognize two (Hultén, 1942; Porsild, 1951; Gjaerovoll, 1958; Anderson, 1959) or three (Stebbins, 1930; Raup, 1947) subspecific entities in the far Northwest with some disagreement about nomenclature. Löve and Löve (1965) have attempted to resolve the differences and relate the taxonomy of the group to reported findings of two principal cytological races, 2n = 56 and 2n = 42, in North America. They concluded that *C. canadensis* s. str. should be restricted to the hexaploid level and that the octoploids should be referred to *C. langsdorfii* (Link) Trin. Later these authors (Löve and Löve, 1966), concurring with Tzvelev (1965), combined *C. langsdorfii* with *C. purpurea* (Trin.) Trin. of Eurasia, it therefore becoming *C. purpurea* ssp. *langsdorfii* (Link) Tzvelev. But this treatment did not encompass the tetraploids (2n = 28) reported in eastern Asia as *C. langsdorfii* (Tateoka, 1954; 1967; Sokolovskaja, 1963). Löve and Löve (1965) considered these tetraploids to be *C. angustifolia* Kom.

However, the report of tetraploid *C. langsdorfii* merits further consideration. Seed for the type material of *C. langsdorfii* presumably originated on Kamchatka Peninsula in eastern Asia. Subalpine meadows in which bluejoint is an important component occur there that are very similar to those in portions of southwestern Alaska (Hultén, 1937a). My investigations reveal that Alaskan bluejoint is a complex consisting of three euploid races, the most abundant being tetraploid, new to the records for North America. These findings justify a taxonomic review of the group. Further, the chorology of the three Alaskan races lends itself to some interesting interpretations regarding the glacial history of the region and its effects on plant survival and migrations.

METHODS

Chromosome counts were obtained on root tips taken from vegetative material collected in the field and grown in the greenhouse. The tips

were soaked in ice water for 16–20 hours, fixed in 3:1 alcohol and glacial acetic acid solution, hydrolyzed in 1N HC1 at c. 60°C for 8–12 minutes, and stained in Feulgen prior to squashing in aceto-carmine. A few counts were made on pollen mother cells collected in the field, fixed in 3:1 solution and smeared in aceto-carmine.

Specimens were analyzed morphologically for the following characters: 1, length of inflorescence; 2, length of spikelet; 3, length of lemma; 4, ratio: point of awn attachment measured from base of lemma/length of lemma; 5, length by which awn exceeds lemma; 6, length of an anther; 7, length of ligule; and 8, width of leaf.

Results and Discussion

Cytology and distribution. Tetraploid and hexaploid races of bluejoint dominate in Alaska. Octoploids appear to be rare except in particular circumstances. Hybrids between the races also are rare, only a single presumed hybrid ($2n = 49$) having been found.

Counts were obtained on the following Alaskan specimens (mainly AES) with all but one of the collections made by the author.

$2n = 28$: W and SW Alaska: Galena, *727A33, 727A38;* Bishop Rock, W of Galena, *727A4;* Poorman, S of Ruby, *621D44, 621D30, 621D31;* Lake Minchumina, N of McKinley Park, *619D29, 619D30, 619D31, 619D32;* Farewell, SE of McGrath, *619D16;* Medfra, E of McGrath, *621D39, 621D41;* McGrath, *622D2;* Takotna, W of McGrath, *621D5;* Colorado Creek, NW of McGrath, *621D6, 621D7, 621D8;* Flat, E of Holy Cross, *621D20, 621D21, 621D22, 621D23, 621D24;* Stony River, on Kuskokwim R., *620D1;* Sleetmute, on Kuskokwim R., *620D15;* Red Devil, NW of Sleetmute, *620D9;* Aniak, lower Kuskokwim R., *620D53;* Anvik, on Yukon R., *620D27;* St. Michael, S coast of Norton Sound, *620D24, 620D44, 620D46;* Stebbins, W of St. Michael, *620D32;* Togiak W of Dillingham, *822D2, 822D6;* Dillingham, *822D14;* Ekwok, NE of Dillingham, *822D15, 822D17, 822D18;* King Salmon, *823D7, 823D10, 823D29;* Iliamna, *823D17, 823D19.*

Cook Inlet drainage region: meadow N of Homer, *712C26;* subalpine grassland E of Anchor Point, *521B1, 521B2, 521B3;* between Kenai and Soldotna, *712C15;* Funny River road E of Soldotna, *105C1, 105C4;* Alyeska, ski lodge SE of Anchorage, *86D1;* cleared areas vicinity of Palmer, *526A1, 526A2, 423B1, 423B2, 816B2, 816B3, 816B4;* Little Susitna Valley N of Palmer, *715B1, 715B2, 98D9, 927D2;* homestead W of Wasilla *921C5;* Skwentna airstrip, Susitna Valley, *619D24, 619D25;* Chelatna Lake W of Talkeetna, *622D7, 622D11, 622D14;* Peters Creek W of Talkeetna, *71A25, 71A26;* Montana Creek S of Talkeetna, *72A10.*

Gulkana and Copper River basin: Mile 15.5 Tok Hwy. N of Gakona, *817D12;* N of Paxson, *922C6;* Tangle R. campground W of Paxson, *926C6;* along Denali Hwy. about 54 miles NW of Paxson, *723B1.*

Tanana River drainage: Mile 17 Taylor Hwy., *818D48, 818D34;* Mile 4 Taylor Hwy., *818D9;* Alaska Hwy. near Tok Juncton *818D3;* Mile 115 Tok Hwy. S of Tok Junction *818D42;* Mile 295 Richardson Hwy. NW of Delta Junction, *923C2;* Mile 310 Richardson Hwy., *923C3;* Mile 312 Richardson Hwy., *710A1;* Fairbanks, *730A1;* Mile 87 Steese Hwy. N of Fairbanks, *924C1.*

$2n = 42$: Western and southwetern Alaska: McGrath, *622D4;* Dillingham, *822D11.*

Cook Inlet drainage region, alpine tundra: Lazy Mt. E of Palmer, *725D10;* Eklutna Vally SW of Palmer, *728D17, 728D16;* Eagle R. valley SW of Palmer, *97D9.*

Gulkana and Copper River Basin: Eureka Lodge area, Glenn Hwy. SW of Glennallen, alpine tundra, *819D10;* Mendeltna Creek, SW of Glennallen, *82C3;* Mile 180 W of Glennallen, *82C19, 82C20, 817D4, 817D8;* Mile 181.5 W of Glennallen, *719B16;* along Richardson Hwy. 1 mle S of junction with Glenn Hwy., *731B7;* Copper Center, *731B10, 819D1, 819D2, 819D6;* McCarthy, *815C21;* along road between McCarthy and Kennecott, *815C7;* Tangle R. campground W of Paxson, *926C5;* 5 mile N of Paxson, *624B12, 922C5, 922C7, 922C8;* Mile 45 Tok Hwy. N of Gakona, *817D16;* Mile 68.5 Tok Hwy., *817D26;* Slana, near junction Tok Hwy. and Slana cutoff, *Dickson* & *Taylor* Aug. 10, 1961.

Tanana and Yukon R. drainages: Mile 30 Taylor Hwy. N of Tok Junction,, *818D23;* Mile 312.7 Richardson Hwy. NW of Delta Junction, *925C5;* Fairbanks, near international airport, *818B19, 818B21;* Manley Hot Springs, *626B12;* Birch Creek S of Circle along Steese Hwy., *924C11;* 1 mile S of Circle, *924C16;* Circle, terminus of Steese Hwy., *924C22.*

2n = 49: Copper Center Lodge area Copper River Valley, *83C11.*

2n = 56: Western Alaska: Bishop Rock, along Yukon R. W of Galena, *727A3, 727A21.*

Upper Cook Inlet region, alpine tundra, southcentral Alaska: Lazy Mt. E of Palmer, *725D2, 725D4, 725D5, 725D18, 725D20;* Little Susitna Valley N of Palmer, *98D3.*

Upper Copper River Drainage: Mile 68.5 Tok Hwy. S of Mentasta Pass, *817D27.*

The tetraploid race predominates in Alaska's southwestern and southcentral coastal regions and probably northward along the coast at least to the Seward Peninsula (fig. 1). The extent of its occurrence beyond the Tanana River drainage in the drier Interior of Alaska is not known, but only hexaploids and octoploids have been reported so far across Canada (Bowden, 1960; Löve and Ritchie, 1966; Nygren, 1954). Hexaploids are present in the upper Yukon River drainage of Alaska and may dominate there, but further sampling is needed. Both hexaploids and tetraploids are well represented in the Tanana Valley from the Canadian border to Fairbanks and in the relatively dry Copper River and upper Susitna River drainages south of the Alaska Range. A few hexaploids were found in alpine landscapes of the coastal southcentral area. The octoploid has been collected only at four locations — in westcentral Alaska, in eastcentral interior, and at two locations on alpine slopes of the upper Cook Inlet area. Occurrence of a possible hybrid between hexaploid and octoploid races at Copper Center implies the presence of octoploids there. The Arctic, Aleutian Islands, and southeastern panhandle have not been investigated cytologically as yet.

Of particular interest is the chorology of the three races in the upper Cook Inlet area. Dense stands of tall-growing bluejoint occur on burnedover timberland and in the subalpine zone above timberline throughout coastal southcentral Alaska. The bluejoint of these stands is tetraploid as determined by a large number of counts. However, octoploids and hexaploids were found in the alpine zone of the Chugach and Talkeetna Mountains near Palmer. Octoploids and hexaploids appear restricted to alpine sites in this area while tetraploids clearly have the advantage in occupying disturbances and dominating certain herbland communities at lower altitudes.
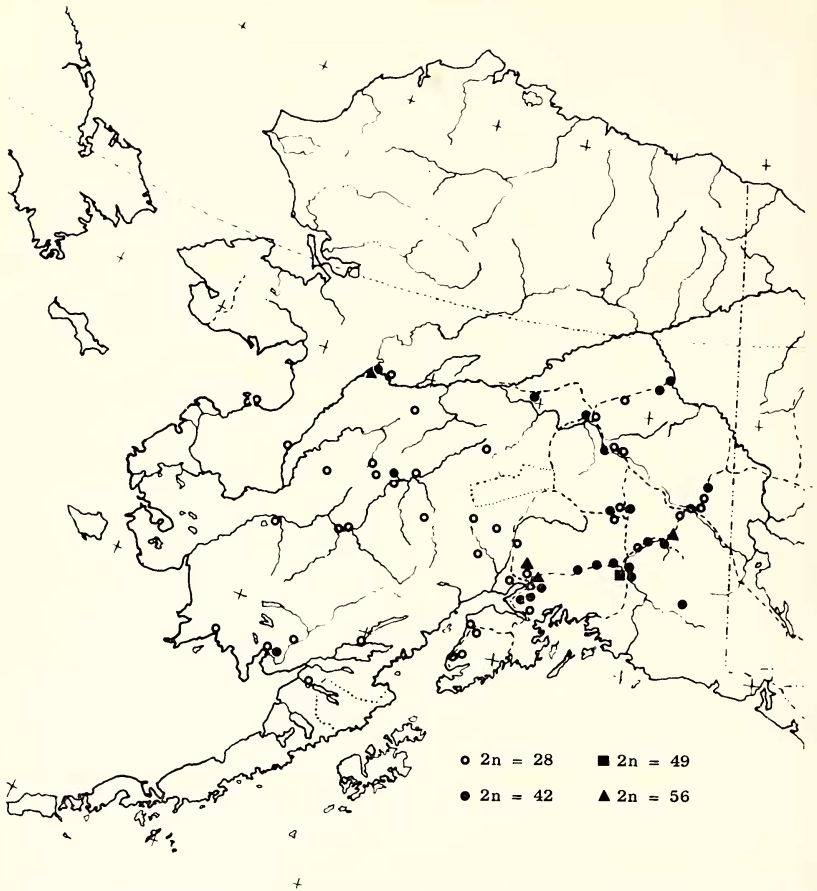
Fig. 1. Distribution of specimens of the *Calamagrostis canadensis* complex in Alaska on which chromosome counts were obtained.

MORPHOLOGY. *Calamagrostis canadensis* is distinguished by its relatively stout rhizomes; generally tall robust culms, occasionally branched, with 3–6 nodes; relatively long, wide leaves; more or less open panicle; glumes with scabrous hairs throughout, often tending to diverge when empty; and thin membranous lemma with delicate awn and long, generally widely spreading callous hairs.

Representative plants of the different races are shown in Fig. 2. Inflorescence form varies a great deal within each race (fig. 3), some of the variation obviously being related to environmental conditions. Clonal material collected at Galena, when grown in a fertilized experimental garden at Palmer, differed tremendously from its depauperate counterpart collected in the field (fig. 3, e and f), as did to a lesser extent material from the vicinity of the Fairbanks International Airport (fig. 3, n and o). Some of these abnormally depauperate individuals resemble *C.*

Fig. 2. Representative vouchers of four chromosome races of *Calamagrostis canadensis* complex in Alaska.

angustifolia in Komarov (1934), but the spikelet characteristics are definitely those of *C. canadensis*. Circumstances appear to require their assignment to *C. canadensis*.

Other workers have had varying success in separating the different
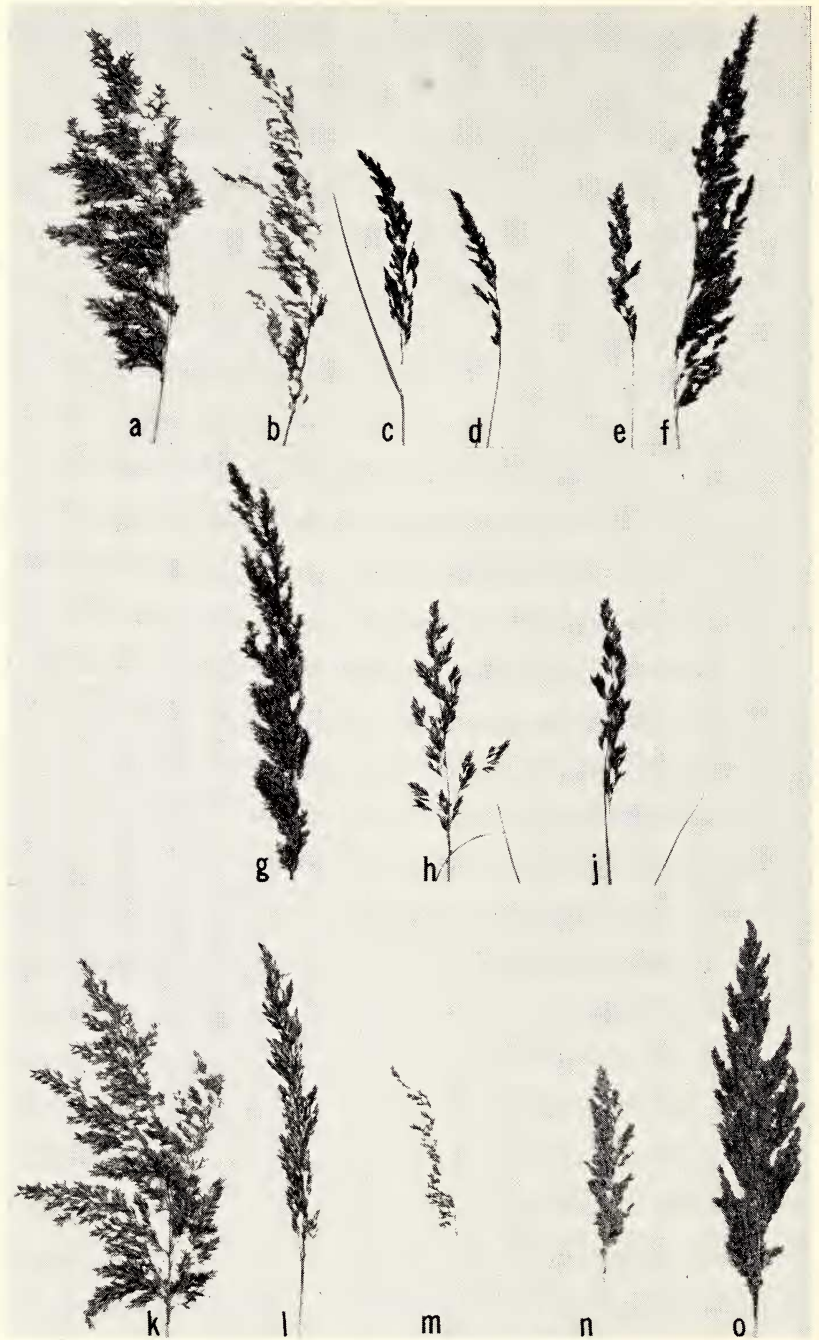
chromosome races. Bowden (1960) concluded that his hexaploid and octoploid plants of northern Canada could not be separated morphologically. Löve and Löve (1965), on the other hand, found the octoploids in the alpine zone of Mt. Washington, New Hampshire, clearly distinguishable from the hexaploids lower on the mountain. Similarly, in the current study spikelet measurements of the octoploids from alpine regions near Palmer were distinctly longer than the bulk of the tetraploids and the few hexaploids found in the same area.

No good qualitative differences were found, however, for distinguishing the races and all overlapped in their measurements (fig. 4 and table 1). Overlapping between the tetraploids and hexaploids is so great as to preclude considering separating these two. The apparent separation of the octoploid is confounded by the occurrence of an ecotypic trend in sizes of plant parts. Those in the interior tend to have smaller parts than those in the coastal regions; for instance, spikelet length of 14 tetraploids of the Cook Inlet region averaged 4.13 mm compared with 3.60 mm for 15 tetraploids of the more northern interior. The 3 octoploid specimens from the interior averaged 4.6 mm, 3.5 mm, and 2.0 mm for spikelet-, lemma-, and anther-length, respectively. Except for anther length these values are within a standard deviation of the average values determined for the hexaploids (table 1). A number of plants analyzed from the Southeast and the Aleutian Islands, cytology unknown, had particularly long spikelets, those from the Aleutian Islands averaging well above the measurements obtained on the octoploid vouchers. A teraploid composition is indicated for the Aleutian Island population (fig. 1), although it may be otherwise. Thus, any effort to differentiate the cytological races morphologically must take into consideration geographic occurrence.

TAXONOMIC DISPOSITION. There is an obvious contradiction in the various interpretations of the *langsdorfii* type. Hultén (1942; 1962) differentiates ssp. *langsdorfii* from ssp. *canadensis* by its longer spikelets, larger panicle, broader leaves, and taller growth. He considers it represented across North America but in Alaska more coastal in its occurrence than ssp. *canadensis*. Löve and Löve (1965; 1966), and others, concur with Hultén in associating *langsdorfii* with the more robust growth habit; further, these authors assign it to the octoploid level.

It appears, however, that the tetraploid material of eastern Asia and that of Alaska are conspecific and relate to the type material of *langsdorfii*. Moreover, the tetraploids as a rule have smaller spikelet measurements

FIG. 3. Variation in inflorescence form and size in the different races of *Calamagrostis canadensis* in Alaska:

2n = 28: a, *Mitchell 922C8;* b, *921C5;* c, *712C15;* d, *96D1;* e, *727A38;* and f, clonal material of *727A38* grown in experimental garden at Palmer.

2n = 56: g, *727A21;* h, *98D3;* and j, *725D20.*

2n = 42: k, *292C7;* l, *82C20;* m, *922C5;* n, *818B21;* and o, clonal material of *818B21* grown in experimental garden at Palmer.
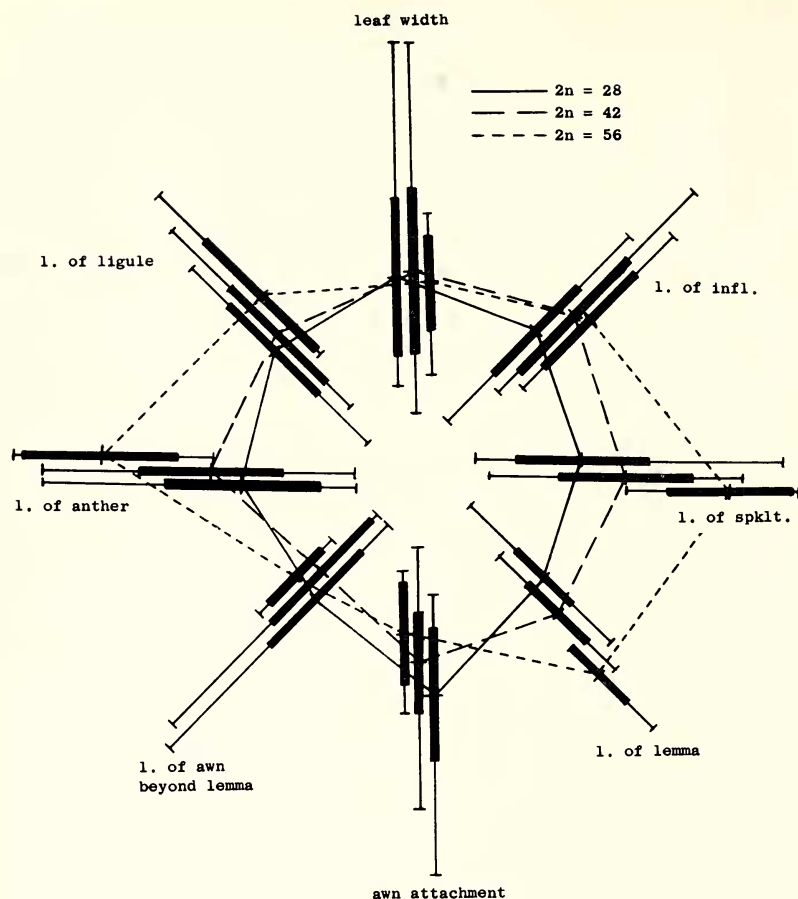
Fig. 4. Polygonal representation of morphological analysis of three chromosome races of *Calamagrostis canadensis* in Alaska based on information contained in Table 1. Total range, mean, and range of two standard deviations represented for each character. Means are interconnected by lines for each race.

than the octoploids and apparently are restricted to eastern Asia, Alaska, and possibly the Yukon Territory and coastal regions to the south of Alaska.

Biologically there may be reason to recognize all three races as specific entities. But morphological considerations preclude the separation of the tetraploid and hexaploid races. In some local areas floral parts may serve, to a certain extent, to separate the octoploid from the other two races. This is much less certain, however, as collections from different areas become involved. In view of the small sample of octoploids so far considered I believe formal recognition of the three races should be deferred until their ranges and morphological distinctions are better delineated.

TABLE I. QUANTITATIVE ANALYSIS OF THREE CHROMOSOME RACES OF THE
CALAMAGROSTIS CANADENSIS COMPLEX.

Number of specimens of each race analyzed: 37 of 2n = 28, 33 of 2n = 42, and 8 of 2n = 56.

Character	Chromosome Race, 2n =	Range	Mean	S.D.	Range of Two S.D.
Leaf width, mm	28	3.0 – 9.0	4.9	1.39	3.5 – 6.3
	42	2.5 – 8.0	5.0	1.42	3.6 – 6.4
	56	3.2 – 6.0	4.8	.82	4.0 – 5.6
Length of inflorescence, cm	28	6.0 – 18.0	11.9	2.83	9.1 – 14.7
	42	8.5 – 21.5	13.5	3.63	9.9 – 17.1
	56	9.5 – 19.5	14.0	3.14	10.9 – 17.1
Length of spikelet mm	28	3.0 – 5.7	3.9	.56	3.3 – 4.5
	42	3.1 – 5.3	4.3	.59	3.7 – 4.9
	56	4.3 – 5.8	5.2	.55	4.7 – 5.8
Length of lemma, mm	28	2.0 – 3.7	2.9	.34	2.6 – 3.2
	42	2.5 – 3.9	3.2	.36	2.8 – 3.6
	56	3.5 – 4.5	3.8	.36	3.5 – 4.2
Awn attachment/length of lemma	28	.16 – .88	.41	.17	.24 – .58
	42	.03 – .71	.33	.13	.20 – .46
	56	.09 – .47	.26	.13	.13 – .39
Length by which awn exceeds lemma, mm	28	0.0 – 1.8	.60	.38	.22 – .98
	42	0.0 – 1.7	.45	.40	.05 – .85
	56	0.3 – 0.9	.60	.24	.36 – 8.4
Length of anthers, mm	28	1.1 – 2.2	1.5	.27	1.2 – 1.8
	42	1.1 – 2.2	1.6	.24	1.4 – 1.8
	56	1.6 – 2.3	2.0	.27	1.7 – 2.3
Length of ligule mm	28	3.5 – 10.0	6.9	1.61	5.3 – 8.5
	42	4.5 – 11.0	7.2	1.79	5.4 – 9.0
	56	6.0 – 12.0	8.2	2.10	6.1 – 10.3

PHYTOGEOGRAPHIC CONSIDERATIONS. Theories on plant survival and migration in glacial and post glacial times propose the revegetation of glaciated southcentral Alaska by plants migrating from the unglaciated interior and the western coastal and exposed Bering Strait region (Hultén, 1937; Heusser, 1967). Heusser also has proposed the survival of plants in small refugia along the southern coast of Alaska. Migration of the octoploids from the interior to their current position in the Cook Inlet area would require their traversing expanses that today are occupied by the obviously more aggressive hexaploids and tetraploids. Some evidence of a migrational history was found in the occurrence of an octoploid plant *(Mitchell 817D27)* on deglaciated terrain at the edge of a ponded kettle near the Mentasta Pass of the Alaska Range. A hexaploid *(Mitchell 817D26)* was found at the same site.

Certainly with a more comprehensive effort the known distribution of the octoploid would become less disjunct than represented in Fig. 1, but it obviously is rare to infrequent through much of Alaska. Octoploid bluejoint would appear to fit Hultén's (1937b, p. 20) description of a taxon losing its variability through periodic reductions by glacial ad-

vances, thereby becoming rigid and unable to spread. I think it unlikely that the current distribution of the octoploid represents a range reduction following a postglacial migration from interior Alaska. Rather, its presence in the alpine regions of the upper Cook Inlet area appears to be that of a relic surviving a more extensive distribution attained prior to the late glacial period. (Also see Löve (1959) concerning the origin and distribution of high polyploids in the pre-Pleistocene and early Pleistocene periods.) I hold a similar view for the octoploids found in west-central Alaska on Bishop Rock, a conspicuous knob in the flats of the Yukon River west of Galena, where a possible relic brome also was discovered (Wilton, 1965; Mitchell and Wilton, 1966). Bishop Rock and other heights in this unglaciated area contain some relatively dry, shaly bluffs that are not subject to the disturbances of the adjacent lowlands and which support plants that do not occur in the more moist, wooded uplands of the area. These are suitable sites for the persistence of relics adapted to their particular conditions.

In the upper Cook Inlet area tall herbaceous and shrubby subalpine communities extend above timberline to the limits of well marked glacial morainic features (Mitchell, 1968a). Karlstrom (1964) cited 2,000 ft. as the elevation of the lateral moraines of the late Wisconsin ice advances on the upper Kenai Peninsula. Moraines occur at about 2,800 ft. on the Chugach and Talkeetna Mountains north of Anchorage. Well developed alpine communities obtain above these morainic features to over 5,000 ft. on the less precipitous mountain slopes. I think extensive areas of these alpine reaches very likely served as refugia for plants during the last ice advances. Finding hexaploid and octoploid races only on what appear to be unglaciated alpine sites in a region where the tetraploid is eminently successful lends support to the theory. Further evidence was found in the occurrence of a tetraploid colony *(Mitchell 927D2)* on an alpine site, about 3,700 ft., that obviously had been glaciated. This suggests a cytological distinction between populations in the upper Cook Inlet region in relation to duration, those of relatively recent origin on glaciated terrain being tetraploid and those of longer duration on unglaciated terrain being hexaploid or octoploid. This theme concerning the existence of nunataks in southcentral Alaska (Mitchell, 1968b) will be developed more thoroughly in a future article.

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NEW RECORDS OF MYXOMYCETES FROM CALIFORNIA. III.

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The number of species of slime molds reported to date in California is 180. Ten new records are listed in this paper. This brings the total number of Myxomycetes reported in print as occurring in California to 190 species. All collections cited here (MICH) are those of the senior author. The names of the organisms are those accepted by Martin (1949) and the numbers are those of the senior author. This investigation was supported by National Science Foundation Grant GB-5799.

We wish to express our appreciation to Travis E. Brooks of the University of Kansas for verifying the identifications of some of the more difficult collections.

Liceaceae

Licea biforis Morgan. On decaying bark, 2 miles west of Child's Meadows, 4,400 feet elevation, Tehama Co., *2747,* Apr. 16, 1966. This species is distinctive in that it is the only member of the genus with sporangia which are repent, fusiform and open by a single longtitudinal slit. Most descriptions give the color as yellow-brown, in this collection the sporangia are black and the depressed longitudinal slit is light tan. Its favorite habitat is stated as being the inner layers of dead bark. The fruiting bodies in this collection are on the outer surface of coniferous bark. This taxon has a very scattered distribution pattern, being known in this country only as far west as Kansas. However, it is probably fairly common. Its rareness is undoubtedly due to its inconspicuousness and may occur throughout the United States.

Licea tenera Jahn. On sheep dung, 3 miles south of Chico, Butte Co., *6238,* May, 1967, developed in a damp chamber. This species is mainly known from moist chamber developments. The type collection consists of approximately a dozen sporangia. The California material fits the type material in that the sporangia are sesile, globose, orange and inde-